

**Life History of the Wood Frog,
Rana sylvatica LeConte (Amphibia: Ranidae),
in Alabama**

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ABSTRACT.— A life history study of the wood frog, *Rana sylvatica* LeConte, was conducted from February 1978 to January 1980. All populations studied were in the Blue Ridge and Piedmont physiographic provinces of Alabama, mostly in semideciduous forests along the flood plains of major streams. Breeding activity occurred from mid-January to late February and coincided with the onset of warm winter rains. Most breeding occurred in semipermanent woodland pools. *Ambystoma opacum* and *A. maculatum* were consistent breeding associates. Usually present were *Notophthalmus viridescens*, *Hyla crucifer*, *Pseudacris triseriata*, *P. brachyphona*, and *Rana sphenocephala*. Mean clutch size in *R. sylvatica* was 496. Diameters of eggs and jelly envelopes are the largest reported for this species. Analysis of stomach contents indicated that adult frogs are opportunistic terrestrial feeders, but they apparently do not feed during the short, explosive breeding season.

The wood frog, *Rana sylvatica* LeConte, is a small to medium-sized ranid frog with an extensive geographic range. Martof and Humphries (1959) reported its range as extending over approximately 4,044,000 square miles (more than 10,000,000 km²) from Alaska to Georgia. This range is exceeded in North America only by that of the *Rana pipiens* complex, which actually consists of several species. Its broad distribution and the relative abundance of *R. sylvatica* over most of its range have prompted considerable research. Most information concerning its life history appears as scattered notes in general references, in papers presenting distributional information or ecology, in studies on amphibian community structure or reproductive behavior, and in accounts in various state herpetological publications.

Rana sylvatica was first discovered in Alabama in 1974 (Mount 1975). Its presence was documented by three specimens from Mt. Cheaha, Cleburne County, in the east central part of the state. Prior to Mount's record, the southernmost locality for *R. sylvatica* was thought

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to be in northeastern Georgia, approximately 160 km northeast of the Alabama locality. The collection of additional specimens south of Mt. Cheaha and the paucity of information on Alabama populations provided the impetus for the present study. Our attention focused on features of the frog's life history, for a cohesive study of this type (especially in the southern part of the range) was lacking. Furthermore, the biology of any organism at the terminus of its range may provide insights into the adaptive significance of geographic variation in life history parameters.

MATERIALS AND METHODS

Considerable effort was devoted to locating potential breeding ponds and breeding populations. Searching was confined chiefly to the Blue Ridge physiographic province and the upper sections of the Piedmont Plateau.

Wood frogs were collected by hand in breeding ponds and on highways during warm rains. Temperatures of water, air, or both were taken with a field thermometer at the time of collection. Most specimens were killed in 20% chloroform, then positioned and fixed in 10% formalin for at least 72 hours. Formalin was injected into the body cavity to preserve food and reproductive organs. Individuals were later transferred to 70% ethanol for permanent storage in the Auburn University Vertebrate Museum.

The stomach and intestine of each frog were removed, slit longitudinally, and the contents washed into a culture dish. All food items were examined under a dissecting microscope and identified to the lowest possible taxon. The volume of food items was not determined. Ovaries or ovisacs were removed and their percentages of total body weight calculated. Ovarian or ovisacal eggs were counted, if present, and then stored in 70% ethanol.

Snout-vent lengths (SVL) were determined by measuring from the tip of the snout to the posterior edge of the urostyle. Tibiofibula lengths (TFL) were taken by measuring the maximum length of the tibiofibula when the shank was completely flexed upon the thigh (Martof and Humphries 1959), and ratios of TFL to SVL were calculated. Snout length, defined as the distance from the anterior edge of the eye to the nostril, and snout height, taken as the straight-line distance from the nostril to the edge of the upper lip (Ruibal 1957), were also measured. All measurements were made with dial calipers to the nearest 0.1 mm after specimens had been kept in alcohol for at least 3 weeks.

Information on reproduction was obtained primarily from field studies. Notes were made on calls of males, egg deposition, clutch size,

egg development, egg mortality, and egg predators. Clutch size was determined by counting the number of eggs in six egg masses and by volumetric displacement of four additional egg masses. Estimates from volumetric displacement were obtained by placing an entire egg mass in a 1-l graduated cylinder containing 200 ml of water. The volume of water displaced by each egg mass was recorded and then multiplied by a standard displacement volume, obtained previously for 10 eggs, to calculate the number of eggs present in the clutch. Larval development in the field was monitored to obtain growth and mortality data. A series of 10 or more tadpoles was collected at one pond during 1979 at varying intervals until no more tadpoles could be found. All were immediately preserved in 10% formalin, then measured and staged in the manner recommended by Gosner (1960). *Rana sphenocephala* tadpoles were also collected in the same ponds at the same times so that developmental rates between the two species could be compared.

RESULTS AND DISCUSSION

HABITAT AND RANGE IN ALABAMA

Wood frogs were collected in five counties in east central Alabama (Fig. 1). Except those on or near Mt. Cheaha, Cleburne County, all collecting localities were near mesic semideciduous forests along the flood plains of large streams. Several frogs collected on Mt. Cheaha were considerable distances from running water, but were never far from mesic sites.

All frogs were collected from localities in the Blue Ridge and Piedmont Plateau physiographic provinces. The floristic and geologic components of these areas have previously been described (Harper 1943, Hodgkins 1965, Johnson and Sellman 1975). The Blue Ridge, as used here, is synonymous with the Blue Ridge herpetofaunal province described by Mount (1975) and the Mountain Forest Habitat Region defined by Hodgkins (1965) and Johnson and Sellman (1975). From a geological standpoint, the terms "Blue Ridge" or "Mountain" may be inappropriate, for the general consensus among geologists is that the Blue Ridge province terminates in northern Georgia. However, the vegetative distribution patterns and faunal components differ sufficiently from the Ridge and Valley province and Piedmont to warrant recognition of the Blue Ridge as a separate entity in Alabama (Johnson and Sellman 1975, Mount 1975). All Piedmont localities for breeding ponds and adult frogs were in the northern subdivision known as the Ashland Plateau. To the north, this part of the Piedmont makes contact with the Blue Ridge, but the transition is gradual with a continuous gradation of the Piedmont into the uplands. The southern subdivision

of the Piedmont, known as the Opelika Plateau, is geologically less complex. The different surface configurations and geological structures in the two plateaus have resulted in some differences in vegetation distribution (Johnson and Sellman 1975, Golden 1968). Mount (pers. comm.) stated that his more recent studies of the herpetofauna of this area indicate that a more distinct transition exists between the Opelika and Ashland Plateaus of the Piedmont than between the latter and the Blue Ridge, if a distinction is to be made.

The southernmost locality known for *R. sylvatica* in North America lies just south of the Tallapoosa River in Horseshoe Bend National Military Park, Tallapoosa County, Alabama. The site is near the boundary of the Ashland and Opelika plateaus in the central Piedmont. The southern boundary of the range of the wood frog in Alabama approximates the southern edge of the Ashland Plateau, although it is likely that many populations are isolates.

One wood frog has been collected in Calhoun County, Alabama (L. G. Sanford, pers. comm.), at the northern edge of the Blue Ridge, and represents the northernmost record for this species in Alabama. The known range in Alabama thus extends from the northern edge of the Blue Ridge along its contact with the Ridge and Valley province to the southern edge of the Ashland Plateau in the central Piedmont. Scattered populations probably occur in suitable habitat in that part of the Ridge and Valley province south of the Coosa Valley. Mount (1975) mentioned that wood frogs might occur in the higher elevations of the Appalachian Plateau in extreme northeastern Alabama (Jackson County). If so, they are probably derived from populations that moved southward on the Cumberland Plateau from Tennessee and not from populations in the Blue Ridge.

Known localities for *R. sylvatica* in Georgia are limited to five counties in the Blue Ridge of the northeastern part of the state (Williamson and Moulis 1979; C. W. Seyle, pers. comm.) (Fig. 2). No specimens have been collected in the 160-km-long area between the Georgia and Alabama wood frog populations, apparently because this area of Georgia has been inadequately surveyed (R. E. Daniel, C. W. Seyle, pers. comms.). Since suitable habitat does occur in this area, we feel that the Alabama wood frog populations are continuous with those in northeastern Georgia (Fig. 2). Based on our knowledge of the habitat requirements of this species in Alabama (and in the southern Appalachians), the presumed range in the intervening area is thought to be limited to the Blue Ridge (Blue Ridge, Cohuttas, Talladega Upland subdivisions), the southern part of the Great Valley, and the Upland and Gainesville Ridges subdivisions of the northern Piedmont (see Wharton 1978).

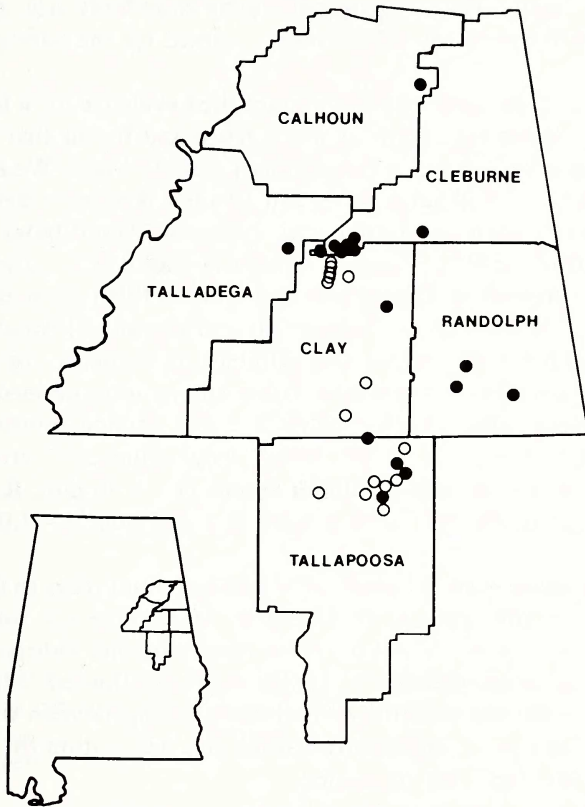


Fig. 1. Known Alabama localities for *Rana sylvatica* determined during this study. Open circles represent breeding localities; inset shows position in the state of counties from which *R. sylvatica* is recorded.

ADULT CHARACTERISTICS

Snout-vent lengths of adult male wood frogs in Alabama averaged 50.0 mm (SD = 5.5, N = 20), and adult females averaged 60.0 mm (SD = 3.16, N = 18). These values are smaller than those given by Martof and Humphries (1959) for wood frogs in northern Georgia and western North Carolina (males: \bar{x} = 54.8 mm; females: \bar{x} = 66.8 mm). Berven (1982a) discovered size differences along an altitudinal gradient from Maryland (lowland populations) to western Virginia (montane populations). Mountain males and females were larger (males: \bar{x} = 55.3 mm; females: \bar{x} = 64.4 mm) than individuals from lowland populations (males: \bar{x} = 41.7 mm; females: \bar{x} = 47.7 mm). Because Berven hypothesized that selection acted primarily on egg size and that selection for

increased fecundity would secondarily favor large body size, comments on the size of Alabama *R. sylvatica* are reserved for the later section on egg size.

Martof and Humphries (1959) established evidence for a latitudinal gradient in relative leg length in wood frogs and found that the frogs with the longest legs occur in the southern Appalachians. We calculated TFL/SVL ratios for 19 adult males and 19 adult females to determine if this trend was evident in Alabama *R. sylvatica*. Tibiofibulas of males averaged .602 of the SVL, those of females averaged .625—a value identical to that obtained by Martof and Humphries (1959) for both sexes.

Ruibal (1957) reported a latitudinal and altitudinal clinal gradient in snout length for *R. pipiens* and pointed out evidence for a similar latitudinal gradient in *R. sylvatica*. Blunt snouts were defined as those with high height/length (H/L) values (> 1.15), pointed snouts as those with low H/L values (~ 1.00). Wood frogs from northern Canada (locality not given) possessed blunter snouts ($\bar{x} = 1.30$ mm, $R = 1.07$ to 1.50 , $N = 14$) than those from New York ($\bar{x} = 1.11$ mm, $R = 1.00$ to 1.22 , $N = 15$).

Snout lengths were measured on Alabama wood frogs to determine if this apparent cline continued. The mean H/L value was found to be 0.83 ($R = 0.74$ to 0.95 , $N = 37$). These results further substantiate the evidence for a clinal increase in snout length southward. Martof and Humphries (1959) and Martof (1970) described Appalachian wood frogs as having blunt snouts, apparently a subjective description for no quantitative H/L analysis was performed.

The coloration of adult *R. sylvatica* in Alabama is typical of the Appalachian phenotype described by Martof and Humphries (1959). A color photograph resembling the Appalachian phenotype may be found in Behler and King (1979, Fig. 216).

BREEDING PONDS, BREEDING ASSOCIATES, AND BREEDING SEASON

All 14 breeding congregations of *R. sylvatica* found were in shallow (usually < 45 cm), temporary pools in or adjacent to forests. These pools fill with winter rains from December through February. Most were located in semideciduous woods along the flood plains of large streams. Three sites were found in pastures; however, these were bordered by semideciduous woods and probably had been wooded in the past.

Breeding ponds differed in the amount and type of vegetation. Ponds in open (pasture) situations received more sunlight and were generally characterized by vigorous growths of *Eleocharis* sp., *Juncus* sp., and *Carex* spp. Woodland pools generally had fewer rushes and sedges, probably because of reduced sunlight. *Peltandra virginica*, *Sagittaria*

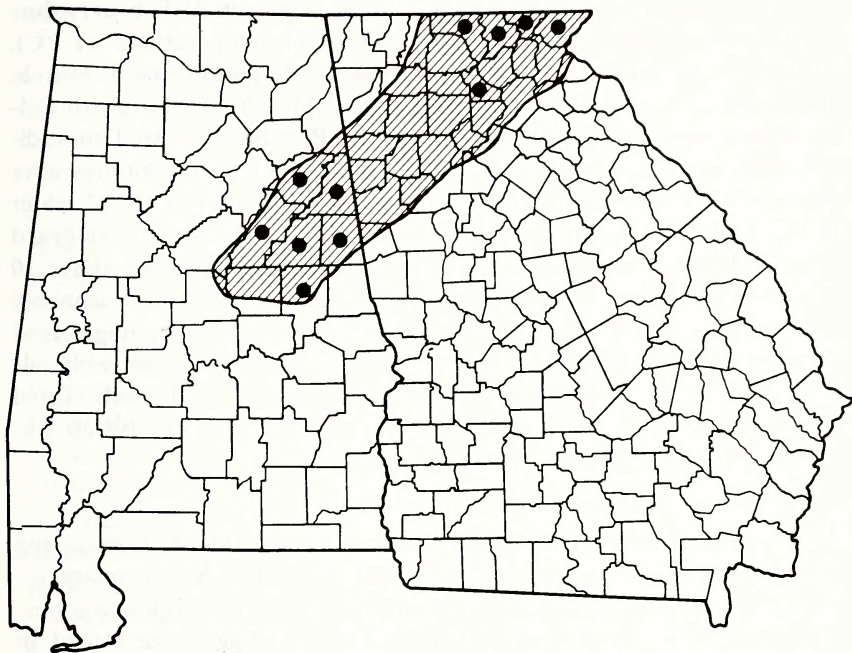


Fig. 2. Distribution of *Rana sylvatica* at the southern terminus of its range. Solid circles indicate counties (not localities) in Georgia and Alabama where specimens have been taken. Presumed range is indicated by hatching (see explanation in text).

latifolia, *Saururus cernuus*, *Sparganium americanum*, and *Ranunculus* sp. were the most common plants in these situations. *Alnus serrulata*, *Quercus* spp., and *Cornus* spp. were usually present along the edges of the pond or in shallow water.

A fairly consistent assemblage of breeding associates was present with *R. sylvatica* during the breeding season. *Ambystoma maculatum* and *A. opacum* were present at every site. *Notophthalmus viridescens*, *Hyla crucifer*, *Pseudacris triseriata*, and *P. brachyphona* were common associates. *Bufo americanus* and *Rana sphenoccephala* were always present in pasture breeding ponds. Collins and Wilbur (1979) reported that, in Michigan, *R. sylvatica*, *H. crucifer*, and *P. triseriata* were breeding associates, particularly in temporary aquatic habitats.

A number of previous accounts described wood frogs as explosive breeders that generally spend only a few days in the breeding ponds (see Seale 1982), and we found this to be true of Alabama populations. Males begin calling with the onset of the first heavy, warm winter rain

from mid-January to late February. Calling began on 21 February during the 1979 breeding season (air and water temperatures 11 °C). Although egg deposition was completed in all ponds by 1 March, males continued to call intermittently until 5 March. Similar postbreeding calling was noted by Waldman (1982). Breeding occurred sporadically between 21 February and 1 March whenever air temperatures were above 5 °C. Vigorous calling occurred on 22 February (air 16 °C, water 14 °C) and 24 February (air 16 °C, water 12 °C). No calls were heard after 5 March even though air and water temperatures were above 10 °C. In 1980, males began calling on 17 January after unseasonably warm weather (air 15.5 °C, water 9 °C, at 2130 CST), but calling ceased early the next morning when the temperature dropped considerably (air 4 °C, water 9 °C, at 0200). Males were in full chorus in all ponds visited on 22 January (air 9 °C, water 12 °C, at 1915). Egg deposition was completed in all ponds by 22 January.

DEVELOPMENT OF OVARIAN EGGS

Females collected throughout the year yielded information on egg development. Body weights of preserved specimens before ovary removal, ovary weights from each specimen, and ovary weights as a percentage of body weights are given in Table 1. Eggs were stored in ovisacs in one female that had completed ovulation. For this specimen, ovisacs (instead of ovaries) with ripe oocytes are expressed as a percentage of total body weight, as indicated.

Examination of females indicated that ovarian weight (expressed as a percentage of body weight) remains fairly constant from early September to late November. No preovulating females were collected immediately prior to the breeding season, but we assume that the greatest increase in size of oocytes occurs during this time (later stages of vitellogenesis). All gravid females collected in the breeding ponds had completed ovulation and mature ova were present in the ovisacs. Ovisacs in a gravid female collected in the breeding pond on 18 January composed 41.7% of the total body weight. Ovarian weight in spent females drops to 3.9 to 5.0% of total weight. The ovaries of a female collected on 14 May were macroscopically similar in appearance to those of spent females. In this female, ovaries equaled 5.3% of total body weight.

Because no females were collected between May and September, we could not determine when oocyte enlargement begins; however, based on the size and appearance of oocytes in females collected during September, we estimate that enlargement begins in July or August. Because ripe oocytes in gravid females compose such a large percentage of total

Table 1. Body and ovarian weights (g) and ovarian weight as a percentage of body weight for adult female *Rana sylvatica* collected in Alabama, at different times of the year.

| Date | Body weight | Ovary weight | Ovary weight as percentage of body weight |
|---|-------------|--------------|---|
| 3 September | 22.4 | 3.3 | 14.7 |
| 29 September | 38.4 | 3.7 | 9.6 |
| 12 November | 24.9 | 3.1 | 12.4 |
| 12 November | 20.4 | 2.9 | 14.2 |
| 23 November | 31.3 | 4.3 | 13.7 |
| 23 November | 27.4 | 4.0 | 14.6 |
| 23 November | 29.1 | 4.8 | 16.5 |
| 17 January (female in breeding pond) | 52.0 | 21.7* | 41.7 |
| 18 January (spent female) | 10.5 | 0.6 | 5.0 |
| 18 January (spent female) | 17.6 | 0.7 | 3.9 |
| 14 May | 13.2 | 0.7 | 5.3 |

* ovisac weight

body weight, an extended period is probably necessary for a female to reach reproductive condition. Redshaw (1972) reported that amphibian oocyte enlargement from 450μ to 1400μ required a period of 9 months.

SEXUAL DIMORPHISM, CALLING, AND AMPLEXUS

Sexual dimorphism is more pronounced during the breeding season. Males are generally much darker than females, the ground color ranging from deep brown to almost black. Howard (1980) noted that this darker color matched the dark color of the water in breeding ponds. Females are usually tan to reddish brown during the breeding season. Darker females are observed occasionally, but they are never as dark as males. The margin of the toe webbing between the digits of the hindlimb is markedly convex in males. The male thumb (first digit on the forelimb) and the musculature in the forelimb are also enlarged during this time, as in other ranid species. Noble and Farris (1929) thought that the additional surface area provided by convexity of the toe webbing allowed males more mobility in the water, a suggestion consistent with the behavior of males during the breeding season. The thumbs of male

wood frogs in Alabama are slightly enlarged throughout the year, becoming more conspicuously so during the breeding season. Toe webbing in females remains concave during the breeding season, a condition found in both sexes throughout the rest of the year.

The call of male wood frogs in Alabama is similar to that described for males elsewhere (Thoreau 1881, Hinckley 1882, Dickerson 1906, Smith 1961, Martof 1970, Minton 1972). It usually consists of two high-pitched croaks or snappy clacks, and may be described as a nasal "back-up," repeated rapidly several times in succession. Solitary males call less frequently, repeating the call only once or twice at varying intervals.

Calling males float or swim at the water surface with forelimbs hanging down and hindlimbs projecting posteriorly. The digits on the hindlimbs are expanded, exposing maximum webbing surface. In large aggregations, males move and interact frequently (see Wright 1914, Noble and Farris 1929, Wright and Wright 1949, Howard 1980, Berven 1981). Calling males are extremely wary and dive below the water surface at slight disturbances, concealing themselves under leaf litter and decaying vegetation on the bottom, or hiding among roots or emergent vegetation. When calling from fairly open water, males are nearly unapproachable. If the pond is small, with emergent vegetation, one can usually approach close enough to observe floating males. Calling males can be heard continuously (though often sporadically) from dusk until dawn, but the chorusing is usually strongest immediately after sunset. Males in almost all Alabama populations call only at night; diurnal choruses were heard at only one breeding pond (W. Baker, pers. comm.). Two lethargic males were collected from the bottom vegetation and leaf litter at one pond during midday. The apparent diel restriction of calling activity is not as conspicuous in more northerly populations (Wright and Wright 1949, Howard 1980, Berven 1981, Waldman 1982). This might be a function of the extremely small population sizes in Alabama and the resultant lack of stimulation by large numbers of conspecifics.

Females in Alabama populations are less conspicuous than chorusing males and usually remain below the surface of the water. This behavior is similar to that noted by Banta (1914) and Noble and Farris (1929). Only one female was seen floating on a pond surface; all others collected in breeding ponds were taken under water while in amplexus. Amplexus is axillary (pectoral), with males clasping females just posterior to the forelimbs.

One interspecific amplexing pair was observed during this study—a male wood frog clasping a female *R. sphenoccephala*. When approached, the male released his hold and swam away. The female, partly covered

with vegetation, remained on the bottom of the pond. The freshly deposited *R. sphenoccephala* egg mass (eggs had completely cleared the cloacal opening) was resting on the posterior surface of the female and obscured her hind limbs. Whether or not the male *R. sylvatica* had extruded sperm over the eggs is not known. The cause of the apparent breakdown in isolating mechanisms in this case is also unknown. Perhaps a breakdown in habitat isolation is a partial explanation. *Rana sylvatica* and *R. sphenoccephala* were found as breeding associates only in sites where the forest had been removed. In Alabama, *R. sylvatica* usually breeds in woodland pools, whereas *R. sphenoccephala* breeds in a variety of open aquatic habitats, as well as in woodland pools. Eggs of both species were found in only one woodland pool during this study. *Rana sphenoccephala* has often been seen breeding in woodland pools in other areas of Alabama (R. H. Mount, pers. comm.). Some ecological separation may occur in the part of the state where the two species are sympatric.

Nelson (1971) mentioned a female *R. sylvatica* that was clasped by a male *R. pipiens*. None of the *R. sylvatica* eggs fertilized by the *R. pipiens* developed beyond gastrulation. Moore (1955) found that development did not proceed beyond gastrulation in experimental laboratory reciprocal crosses of *R. sylvatica* and *R. pipiens*. Interspecific pairing of male *R. sylvatica* with other amphibians in the laboratory was reported by Wright (1914).

OVIPOSITION

The eggs of *R. sylvatica* in Alabama are laid as submerged globular masses, usually attached to vegetation. Often, upper portions of the egg mass become emergent. Moore (1949) pointed out that the deposition of submerged egg masses by northern ranid species (those adapted to cool climates) is an adaptation that helps protect the developing embryos from freezing. The rapid drop in water level that often occurs in temporary pools in Alabama may cause exposure of the egg masses in certain situations. Desiccation then becomes an added mortality factor. The depth of water in which oviposition occurs is fairly consistent, averaging 15 to 20 cm.

Wood frogs characteristically have communal oviposition sites. The advantages of this behavior have been discussed (Wells 1977, Howard 1980, Seale 1982, Waldman 1982, Waldman and Ryan 1983). Communal oviposition sites (COS) were encountered in this study only in breeding ponds with larger populations. The largest such site was in a pond south of Mt. Cheaha where 147 egg masses, arranged in two layers, were found in an area 1.5 x 1 m square. Another COS (65 egg masses)

was in a small woodland pond in northern Tallapoosa County. In both ponds all egg masses were restricted to the COS. The third largest population (60 egg masses) was in a pasture breeding pond, where communal oviposition occurred, but to a lesser extent. In this pond 31 egg masses were in a communal site, and the rest were deposited in small clumps separate from the COS. The 11 other wood frog breeding ponds discovered during this study were characterized by extremely small populations (compare Howard 1980, Berven 1981, Seale 1982, Waldman 1982). The number of egg masses found in each of these ponds varied from 4 to 28, and the tendency toward communal oviposition was less pronounced.

Clutch size varied from 350 to 709 eggs per mass ($\bar{x} = 496$). Ovarian and/or ovisac counts indicated that oviposition may occur once or twice during the breeding season. The number of ovarian eggs per female ranged from 618 to 966. When all eggs are deposited at one time, the resultant egg mass appears as two fused masses, indicating that females empty each ovisac separately. If a female moves to another site after emptying one ovisac, the resultant egg mass represents approximately one-half the ovarian complement. This probably accounts for much of the apparent variability in clutch sizes observed in the field. Even so, there is some variability in reproductive potential, as evidenced by the range in egg complements seen in gravid females. This is probably attributable to a combination of individual and ontogenetic variation. Seale (1982) found no significant difference between clutch size and ovarian egg counts in Pennsylvania wood frogs (clutch: $\bar{x} = 895$; ovarian eggs: $\bar{x} = 840$). Although there are few data available concerning ovarian egg counts, several authors have presented information on clutch size (Table 2). There is some evidence for smaller clutch size in the southern parts of the range, although this trend may be obscured by altitudinal differences (Berven 1982a). Clutch size probably varies in response to different selection pressures throughout the geographic range, creating a chaotic pattern of variation. Furthermore, variation in clutch size should be viewed with respect to differences in adult body size and egg size. At the southern terminus of the frog's range, the probability of egg mortality resulting from freezing is reduced and may be a factor in decreased clutch size. Moore (1949) pointed out that the submerged egg masses of northern species of *Rana* were poorly adapted for higher pond temperatures because diffusion of oxygen would not be rapid enough to supply the metabolic needs of embryos in the center of the egg mass. Thus, the smaller egg masses characteristic of southern populations of *R. sylvatica* would allow a more rapid diffusion of oxygen to these inner embryos. However, Savage (1961) claimed that egg masses possess intercapsular channels and that gaseous diffusion need not take

place through the entire egg mass. If so, smaller clutch size resulting from selective pressures for small egg mass size would be an inappropriate hypothesis.

The eggs of Alabama wood frogs are the largest reported for any population of *R. sylvatica* (\bar{x} = 2.9 mm diam., SD = .08, N = 50). Comparison of these values with previously published information indicates a general trend for egg diameter to increase southward (Table 2.). Berven (1982a) hypothesized that selection has acted primarily on egg size, and that other reproductive traits such as clutch size, body size, and age at first reproduction have evolved secondarily. Different selective pressures in different environments would confer differential selective advantages on particular sizes of eggs, clutches, and adults (see Berven 1982a,b, for discussion).

The large size of eggs in Alabama populations of *R. sylvatica* is probably a consequence of increased fitness (larger size) of larvae hatching from these eggs (see Berven 1982a,b), a phenomenon that would result in faster growth rates and shorter larval periods. In Alabama populations, selection for rapid metamorphosis would probably result from breeding exclusively in temporary ponds. An additional selective pressure for more rapid metamorphosis in *R. sylvatica* may be the concurrent breeding of *R. sphenoccephala* in the same sites. This does not seem to be the case farther north. Berven's hypothesis concerning the relationship of large egg size to large body size is difficult to support with data from Alabama wood frogs. Although egg size is largest in Alabama populations, adults are somewhat smaller than those reported in other parts of the southern Appalachians (see earlier mention). Because determination of different age classes was not possible during this study, size comparisons and determinations of age and size at first (and subsequent) reproduction await further study. Larger sample sizes obtained by future workers will probably help to clarify this situation.

The diameters of egg jelly envelopes for *R. sylvatica* in Alabama are larger than values reported in other parts of the range. Diameters of inner envelopes averaged 6.6 mm (R = 5.4 to 7.2 mm, N = 50); outer envelopes averaged 14.0 mm (R = 12.4 to 17.3 mm, N = 50). Few data are available on more northerly populations (Table 2). The reasons that jelly envelopes of Alabama wood frogs are so much larger than those in northern populations are not obvious. Perhaps jelly deposition is controlled by egg size, with larger eggs receiving more jelly.

EGG FERTILITY, DEVELOPMENT, AND PREDATION

Fertility, although variable, was quite high, and several egg masses exhibited 100% fertility. Three clutches were entirely infertile, perhaps a result of oviposition in the absence of a clasping male. Early mortality

of developing eggs was occasionally observed. These eggs usually were infested with fungi, which probably invaded after egg death rather than having been the cause of mortality.

Wood frog egg masses were easily recognized in breeding ponds by their characteristic shape and the large size of their jelly envelopes. Another distinguishing feature was a greenish color imparted to the jelly envelopes by a unicellular green alga. Dickerson (1906) first noted the presence of this alga and assumed that the relationship was mutualistic. Gilbert (1942) also observed this alga in jelly envelopes of wood frog eggs and identified it as *Oophila amblystomatis*, a species characteristically found in the egg jelly of *Ambystoma maculatum*. Surprisingly, there has been little inquiry into the relationship between wood frog eggs and algae by subsequent workers (see mentions by Pope 1964, Gatz 1973). Although the relationship between *A. maculatum* and *Oophila* has generally been viewed as mutualistic (Gilbert 1942, 1944; Hutchinson and Hammen 1958; Hammen and Hutchinson 1962), a higher rate of mortality has been related to the presence of the alga in some cases (Anderson et al. 1971, Gatz 1973). Further investigation concerning the relationship between the alga and *R. sylvatica* eggs is warranted.

All egg predators observed during this study were invertebrates. Mayfly naiads (Siphonuridae, Ephemerellidae) and isopods (Asellidae) were often present between adjacent egg envelopes within egg masses. Caddisfly larvae (Phryganeidae) fed on the external surfaces of egg masses, and one leech, *Macrobdella decora*, was found feeding on an egg mass. Cory and Manion (1953) found this same leech destroying the majority of wood frog eggs in some situations in Indiana, and thought that its presence in certain populations of *R. sylvatica* might constitute a check on population size. Since only one *M. decora* was observed during our study, the effect of this species on Alabama wood frog populations is probably minimal.

Hudson (1954) reported newts, *Notophthalmus viridescens*, feeding on wood frog eggs in Pennsylvania. This salamander was a potential egg predator in Alabama wood frog breeding ponds, but predation was never observed during our study. The large diameters of egg jelly envelopes of *R. sylvatica* in Alabama populations might reduce newt predation.

HATCHING, LARVAL DEVELOPMENT, AND LARVAL MORTALITY

The length of the period between egg deposition and hatching varies directly with water temperature. Under field conditions, wood frog tadpoles generally hatch in 7 to 9 days after eggs are deposited (water temperatures variable, 5 to 17 °C). Larvae hatch at a fairly advanced developmental stage, usually stage 20 (gill circulation, Gosner 1960) or

Table 2. Reported values for clutch size, ovarian egg count, egg diameter, and jelly envelope diameter of *R. sylvatica*.

| Location | Clutch size | Ovarian egg count | Egg diameter (mm) | Jelly envelope diameter (mm) | Source |
|---------------|--|-------------------|-------------------|---|--------------------------|
| Alaska | $\bar{x}=778$ | | $\bar{x}=1.6$ | | Herreid and Kinney 1967 |
| Manitoba | | | $\bar{x}=1.6$ | | Berven and Gill 1983 |
| Michigan | $\bar{x}=646$ | | $\bar{x}=1.82$ | | Collins 1975 |
| Minnesota | R=1000-3000 | | | | Bellis 1957 |
| New York | R=2000-3000 | | $\bar{x}=1.9$ | inner: $\bar{x}=3.8$ R=3.6-5.8 | Wright 1914 |
| | | | R=1.8-2.4 | outer: $\bar{x}=6.4$ R=5.2-9.2 | |
| | R=2000-3000 | | R=1.8-2.4 | inner: R=3.6-5.8 outer: R=5.2-9.4 | Wright and Wright 1949 |
| Massachusetts | 1380 (one egg mass) $\bar{x}=1019$ | | | | Hinckley 1882 |
| Connecticut | | | $\bar{x}=1.8$ | | DeGraaf and Rudis 1983 |
| Rhode Island | R=1000-3000 | | | | Witschi 1953 |
| Pennsylvania | $\bar{x}=895$ | $\bar{x}=840$ | $\bar{x}=2.29$ | | Dickerson 1906 |
| Indiana | R=2000-3000 | | | | Seale 1982 |
| Illinois | R=2000-3000 | | | | Minton 1972 |
| W. Virginia | | | $\bar{x}=2.0$ | outer (?): R=6.0-9.0 | Smith 1961 Green 1952 |
| Virginia | $\bar{x}=920$ | | $\bar{x}=2.28$ | | Berven 1982a |
| Maryland | $\bar{x}=642$ | | $\bar{x}=1.83$ | | Berven 1982b |
| Missouri | $\bar{x}=621$ | | | | Johnson (pers. comm.) |
| N. Carolina | | | $\bar{x}=2.25$ | | Witschi 1953 |
| Tennessee | $\bar{x}=465$ | | $\bar{x}=2.25$ | | Meeks and Nagel 1973 |
| | | | R=2.1-2.4 | | |
| Alabama | $\bar{x}=496$ R=350-709 | R=618-966 | $\bar{x}=2.9$ | inner: $\bar{x}=6.6$ outer: $\bar{x}=14.0$ | This study |

stage 21 (cornea transparent), and average 10.7 mm ($R = 9.8$ to 11.0 , $SD = .34$, $N = 10$) in length. Meeks and Nagel (1973) found that hatchling size in eastern Tennessee averaged 8.0 mm, but did not indicate developmental stage at hatching. Herreid and Kinney (1967) found that hatching occurred at stage 20 in Alaskan populations.

An easily observed size difference between hatchling *R. sylvatica* and *R. sphenoccephala* allowed us to monitor larval development of these two species at one pond during 1979. Leopard frog tadpoles hatch at slightly earlier stages, usually stage 19 (heartbeat) or stage 20, but are considerably smaller than *R. sylvatica* tadpoles, averaging 6.6 mm ($R = 6.2$ to 6.8 mm, $SD = .17$, $N = 10$) in length. The results obtained from the samples are summarized in Figure 3.

Wood frog tadpoles grew more rapidly than leopard frog tadpoles until about 15 April, at which time the tadpoles of both species were approximately the same length (*R. sylvatica*: $\bar{x} = 40.9$ mm, $N = 10$; *R. sphenoccephala*: $\bar{x} = 40.7$ mm, $N = 10$); however, wood frog tadpoles at this time were 5 to 11 developmental stages beyond leopard frog tadpoles. Leopard frog tadpoles then continued to increase in length, whereas wood frog tadpoles began to decrease as a result of initial tail resorption with the onset of metamorphic climax. Wood frog tadpoles were last collected in the pond on 29 April, at which time most were in stage 42 (both forelimbs erupted) and averaged 40.5 mm in length. Leopard frog tadpoles averaged 53.6 mm in length at this time, with most individuals in stage 35 (toes 1 and 2 joined, others separate). Leopard frog tadpoles collected between 29 April and 5 May revealed that tadpoles of this species continue to grow. Mean length of *R. sphenoccephala* tadpoles collected on 5 May (not shown on graph) was 56.0 mm, at which time larvae were in stage 38 (metatarsal tubercle formation).

It has been shown that wood frog and leopard frog tadpoles may behave as ecological equals (DeBenedictus 1974). The larger size and more advanced stage of development at hatching may give *R. sylvatica* tadpoles some initial competitive advantage over those of *R. sphenoccephala*. The more rapid development of *R. sylvatica* probably represents an adaptation to breeding in temporary pools and might result in some resource partitioning on those infrequent occasions when these two species use the same breeding ponds. Alford and Crump (1982) found size class segregations in *R. sphenoccephala* tadpoles, both in laboratory experiments and field situations, and felt that the negative correlation between large (and/or older) and small (and/or younger) tadpoles indicated habitat partitioning.

Since newly transformed *R. sylvatica* froglets were not collected in the field, the exact amount of time from oviposition until transformation is not known. No wood frog tadpoles were collected on 5 May,

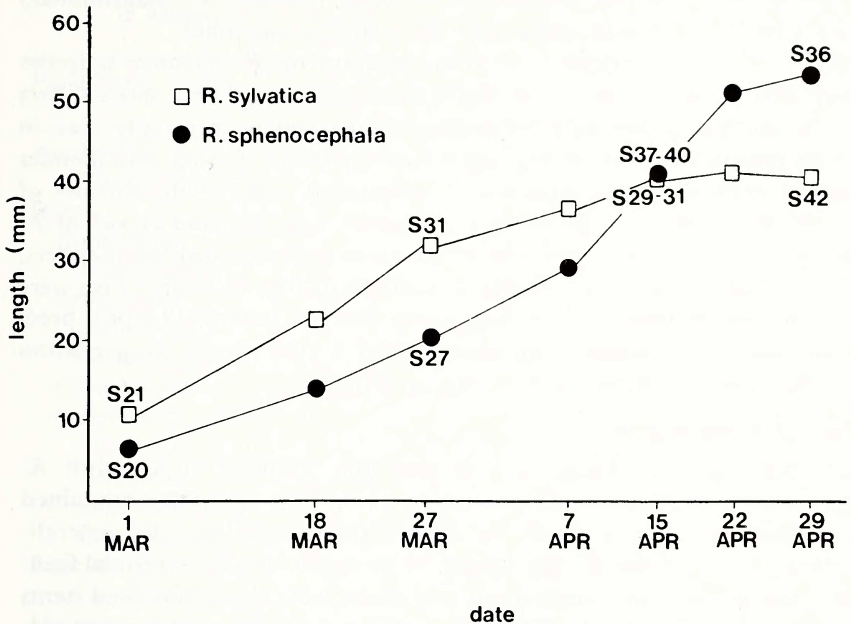


Fig. 3. Larval development of *Rana sylvatica* and *Rana sphenocephala* in Pasture Pond, Tallapoosa County, Alabama. Numerals preceded by the letter S indicate the developmental stage in tadpoles at the time of collection.

however, indicating that all larvae were transformed at this time. This would give a maximum transformation period of 73 days in the field. Most individuals had probably transformed by 29 April (or somewhat earlier); only four tadpoles were collected in the pond at that time. This would indicate a transformation time of about 66 days.

Various vertebrates and invertebrates preyed on wood frog larvae, though not all predators were present at each breeding pond. All invertebrate predators were insects. Adult back swimmers (Notonectidae) and predaceous diving beetles (Dytiscidae) were often seen preying on small tadpoles. Nymphal notonectids and larval dytiscids also probably preyed on wood frog larvae, as observed by Dickerson (1906). Herreid and Kinney (1966) noted extensive predation on wood frog larvae by *Dytiscus* spp. in Alaska. Formanowicz and Brodie (1982) found no survival of stage 42 and younger wood frog tadpoles when subjected to predation by larval *Dytiscus verticalis* in the laboratory. Increased survivorship in older tadpoles and froglets (stage 42 to 46) was attributed to unpalatability, a result of the development of active granular glands during later stages of metamorphosis. Other potential insect predators

present were odonate naiads (Libellulidae, Lestidae, Coenagrionidae) and nymphal and adult giant water bugs (Belostomatidae).

The most significant vertebrate predator on *R. sylvatica* tadpoles appeared to be the larvae of *Ambystoma opacum*. These salamanders were always present in the breeding ponds and were usually seen in close proximity to wood frog egg masses prior to hatching. Salamander larvae probably were attracted to unhatched eggs by movements of developing embryos. Walters (1975) stated that eggs and larvae of *R. sylvatica* were readily eaten by adult newts and marbled salamanders, but neither of these was noted as a predator during our study. Fish were usually absent from the breeding ponds, but one potential tadpole predator, *Lepomis cyanellus*, was encountered in two ponds. No predation by this species was observed during our study.

ADULT FOOD HABITS

We examined stomach and intestinal contents of 42 adult *R. sylvatica* from Alabama. Because only 14 of these specimens contained identifiable food items (Table 3), this analysis is useful only for generalization. Alabama wood frogs appear to be opportunistic terrestrial feeders. Insects, spiders, earthworms, and snails were the major food items present. A scarab beetle, *Eutheola rugiceps*, was discovered in the coelom of one specimen. A large hole in the stomach indicated that the beetle had torn its way through the stomach wall after being ingested (Davis and Folkerts 1980). Neither males nor females collected in breeding ponds contained food. Since all were immediately preserved, we assume that neither sex feeds at this time. Adult wood frogs may not require food during such a short, explosive breeding period.

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Table 3. Composition of stomach contents of 14 adult *Rana sylvatica* collected in Alabama.

| Food items | Percent of stomachs containing item |
|----------------|-------------------------------------|
| Arachnida | |
| Tetragnathidae | 43 |
| Insecta | |
| Homoptera | |
| Membracidae | 7 |
| Orthoptera | |
| Blattellidae | 7 |
| Gryllacrididae | 29 |
| Plecoptera | 7 |
| Coleoptera* | |
| Elateridae | 14 |
| Carabidae | 7 |
| Staphylinidae | 14 |
| Scarabaeidae | 7 |
| Annelida | |
| Lumbridae | 21 |
| Mollusca | |
| Gastropoda | 21 |

* Several beetles were not identifiable.

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